

# Seagrass corridors and tidal state modify how fish use habitats on intertidal coral reef flats

Jean P. Davis<sup>1,2,\*</sup>, Kylie A. Pitt<sup>1</sup>, Andrew D. Olds<sup>1,3</sup>, Alastair R. Harborne<sup>4,5</sup>,  
Rod M. Connolly<sup>1</sup>

<sup>1</sup>Australian Rivers Institute – Coast and Estuaries, and Griffith School of Environment, Griffith University, Gold Coast, QLD 4222, Australia

<sup>2</sup>California Department of Fish and Wildlife, Marine Region, Los Alamitos, CA 90720, USA

<sup>3</sup>School of Science and Engineering, University of the Sunshine Coast, Maroochydore, QLD 4558, Australia

<sup>4</sup>Department of Biological Sciences, Florida International University, North Miami, FL 33181, USA

<sup>5</sup>Marine Spatial Ecology Laboratory and Australian Research Council Centre of Excellence for Coral Reef Studies, School of Biological Sciences, The University of Queensland, Brisbane, QLD 4072, Australia

**ABSTRACT:** Identifying pathways that animals use to move among ecosystems has become a focus for improving conservation planning. The function of habitat corridors in facilitating animal movement among terrestrial ecosystems is well established. By contrast, the role of habitat corridors for the movement of marine animals is poorly understood. We used underwater video cameras to evaluate the effects of seagrass corridors and water depth on fish abundance, and the arrival of prey and predatory species on intertidal coral reef flats in eastern Australia. Cameras were placed in intertidal seagrass and unvegetated habitats during incoming tides and recorded fish that moved across these habitats. We found some evidence that fish were more abundant over intertidal seagrass, particularly garfish *Hyporhamphus regularis ardelio*, striped barracuda *Sphyraena obtusata* and striped grunter *Pelates sexlineatus*, but most species did not appear to use the intertidal seagrass as a corridor. Prey fish were generally more abundant at shallower water depths, whereas predators were more common in deeper water, but many species were present over intertidal flats throughout the incoming tide. Our findings show that the movement of fishes across intertidal flats is dynamic, and depends on the species of interest, the composition of intertidal seascapes and tidal condition. Understanding how biotic and abiotic factors interact to influence fish movement and shape patterns in habitat use is a critical challenge for conservation planning in shallow coral reef seascapes.

**KEY WORDS:** Habitat corridor · Predation refuge · Underwater video · Mangrove

— Resale or republication not permitted without written consent of the publisher —

## INTRODUCTION

The functioning of tropical coastal ecosystems is contingent on processes that occur across multiple habitats (Sheaves 2009). Mobile nekton, especially fish, transfer energy among inshore habitats such as coral reefs and mangroves (Pittman & Olds 2014, Green et al. 2015) via short-term feeding and spawning migrations (Verweij et al. 2006, Hammerschlag et al. 2010) as well as longer-term ontogenetic move-

ments (Jones et al. 2010). The relationship between connectivity and ecological processes has made identifying the pathways that mobile fauna take to move between habitats a primary focus for the conservation of ecosystem function in coastal areas (Nagelkerken et al. 2015).

Fish move across aquatic habitat boundaries via active dispersal, which is influenced by current flow (Caselle & Warner 1996), predation risk (Nanjo et al. 2011) and prey availability (Werner & Hall 1988).

Less is known about the effect of seascape structure on fish movement (Boström et al. 2011). Seascape structure refers to the distribution of habitat patches in marine landscapes (Boström et al. 2011). Understanding the movement of animals along habitat corridors has long been a focus for terrestrial conservation planning (Beger et al. 2010, Gilbert-Norton et al. 2010). Marine conservation could be improved by better understanding how seascape structure similarly facilitates connectivity between habitats for fishes (Olds et al. 2016).

In Moreton Bay, Australia, many fishes use fringing mangroves at high tide (Laegdsgaard & Johnson 1995). Mangroves offer a foraging opportunity for some fish species (Davis et al. 2014) and a nursery habitat for others (Laegdsgaard & Johnson 1995). Seagrass offers a potentially important corridor for movement between subtidal habitats and intertidal mangroves because it offers feeding opportunities (Nagelkerken et al. 2008, Unsworth et al. 2008) and increased protection from predators (Jordan et al. 1997) to fish during intertidal migration. Seagrass habitats function as corridors for marine invertebrates (Micheli & Peterson 1999, Darcy & Eggleston 2005), and this might also be true for fishes in intertidal tropical and subtropical seascapes where fish abundances in mangroves are positively correlated with the proximity of adjacent seagrass habitat (Irlandi & Crawford 1997, Pittman et al. 2004, Lugendo et al. 2007).

Among the fish species in Moreton Bay that move from subtidal habitats to mangroves, those that commonly forage and shelter in seagrass, such as yellowfin bream *Acanthopagrus australis* (Melville & Connolly 2003) and garfish *Hyporhamphus regularis ardelio* (Carseldine & Tibbetts 2005), might be more likely to use seagrass habitat as corridors than fishes that do not gain any benefits from seagrass, such as sea mullet *Mugil cephalus* (Chubb et al. 1981). Thus, we expect species that also benefit from the corridor habitat itself will be more likely to travel along it. While seagrass habitat provides important ecosystem services to many fishes, it may not function as a corridor for all species. Some fishes in Moreton Bay, such as silver-biddy *Gerres subfasciatus*, move among reef flats and mud flats, but are uncommon in seagrass or mangroves (Morton 1990). Therefore, these species are less likely to depend on seagrass corridors, since they move shorter distances from subtidal habitats than fish that regularly access adjacent mangroves.

In macrotidal environments, tidal exchange strongly influences the movements of fish (Krumme 2009),

possibly because prey fishes seek refuge from predators in shallow water at low tide. The paradigm that shallow water habitats (<0.5 m) reduce predation risk for small and juvenile fishes from larger-bodied predators has been reported widely (Rypel et al. 2007, Ryer et al. 2010, Becker et al. 2011, Banikas & Thompson 2012), but has also been criticized because predators can be both diverse and abundant in shallow waters (Sheaves 2001). The influence of water depth on predator–prey interactions is complex (Becker et al. 2011) and may depend on the species and seascapes in question (Baker & Sheaves 2007). For example, predators like flathead (Platycephalidae), barramundi (Latidae), requiem sharks (Carcharhinidae) and hammerhead sharks (Sphyrinidae) can be common in shallow-water zones of tropical estuaries (Baker & Sheaves 2005, 2006, Dorenbosch et al. 2009, Tobin et al. 2014). Predators clearly occupy shallow intertidal habitats; however, little is known about the movement of fish into intertidal habitats, and whether, and how, accessibility modifies patterns of succession with tidal inundation (Harborne 2013). In microtidal estuaries, prey fish migrate during the shallowest part of the tide (Bretsch & Allen 2006, Ellis & Bell 2008, Becker et al. 2012, Kimball & Able 2012). Patterns of succession in the movement of prey and predatory fishes into intertidal habitats have, however, not been examined in macrotidal tropical estuaries.

The aim of this study was to use underwater video arrays to investigate whether fish use intertidal seagrass habitats as corridors when making intertidal movements, and to test for differences in the arrival times of prey fish and their predators during incoming tides (Fig. 1). The following hypotheses were tested: (1) fish abundance differs between continuous seagrass habitat and unvegetated reef flats during the flood tide, (2) fish that are commonly associated with mangrove habitats will be more common on intertidal seagrass than unvegetated reef flat habitat, and (3) prey fish move into the intertidal zone earlier than predatory species.

## MATERIALS AND METHODS

### Study location

Moreton Bay is a subtropical embayment in south-east Queensland, Australia, and has a tidal range of ~2 m. It is a useful model environment to test the importance of benthic habitat corridors for mobile fishes because subtidal fringing coral reefs in the bay

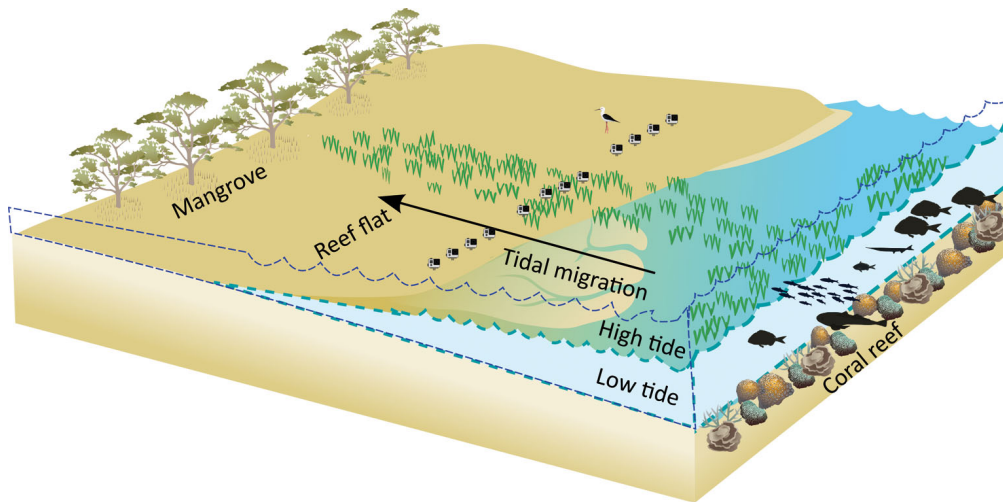


Fig. 1. Overview of the camera array, distribution of habitats and change in tidal depth at the locations sampled (symbols courtesy of the Integration and Application Network, [ian.umces.edu/symbols/](http://ian.umces.edu/symbols/))

are proximal to productive intertidal reef flat and mangrove habitats, which are completely exposed at low tide. Moreover, some fishes found on reefs at low tide are observed in the mangroves at high tide (Olds et al. 2012a) and depend on resources from intertidal habitats for their nutrition (Davis et al. 2014).

Fish abundance was recorded over potential seagrass corridors and in adjacent unvegetated habitats on intertidal reef flats at 3 locations in central Moreton Bay (Coochiemudlo Island, Northwest Peel Island and Western Peel Island; Fig. 2). Reef flats in Moreton Bay are intertidal low-relief coral rubble substrates with sediment and sand deposits, extending from the subtidal edge of the coral reef to fringing

mangroves on the shoreline. Moreton Bay supports 190 km<sup>2</sup> of subtidal and intertidal seagrass beds, and the dominant species is *Zostera muelleri* (Dennison & Abal 1999). Seagrass cover varies throughout the bay dependent on water depth and exposure to tidal flushing (Lyons et al. 2011). Around the bay's coral islands, seagrass typically occupies soft sediment breaks in the reef flat that form between the fringing reef and mangroves. At each location, a continuous strip of intertidal seagrass (*Z. muelleri*), approximately 40 m wide and ~250–500 m long, linked the subtidal edge of the reef to the intertidal mangroves, and was bordered on either side by unvegetated reef flat. Bathymetry was consistent at all locations.

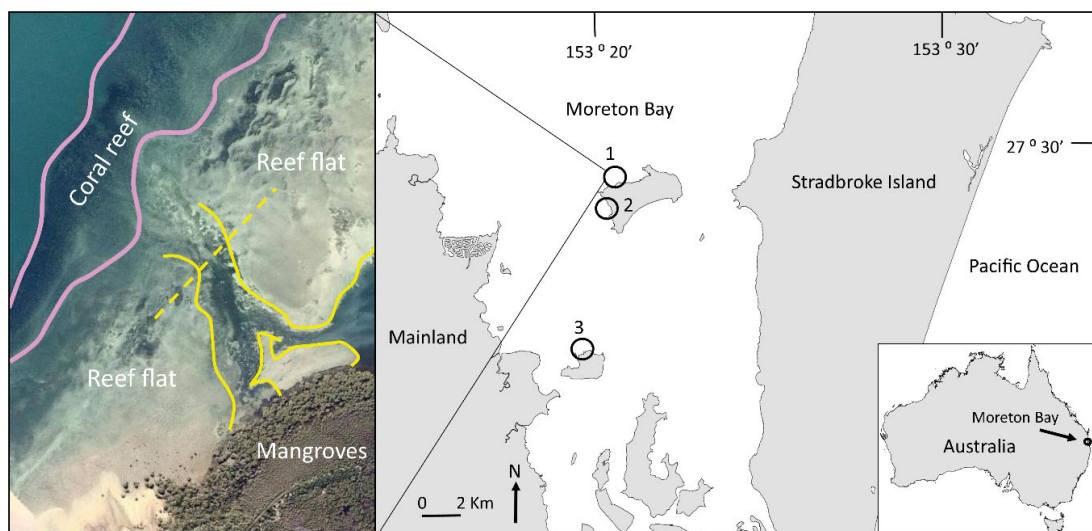


Fig. 2. Positions of survey locations (open circles) in Moreton Bay, Queensland, Australia, including locations 1 (Northwest Peel Island), 2 (Western Peel Island) and 3 (Coochiemudlo Island). Inset: detailed seascape at Northwest Peel Island, with yellow outlines highlighting areas of continuous seagrass habitat and dashed yellow line indicating the location of the camera arrays

## Video deployment

At each location, the abundance of fish over intertidal seagrass and unvegetated habitats was recorded during the first 4 h of the incoming tide using unbaited underwater video cameras (GoPro Hero 4 Silver). Each of the 3 locations was sampled 3 times during the austral spring/summer (October 2013 to January 2014). Cameras were deployed on morning spring low tides (between 05:00 and 09:00 h) to capture the strongest patterns in fish movement (Meynecke et al. 2008) and avoid potentially confounding effects of variations across diel cycles. Cameras were deployed parallel to the shoreline and facing the incoming tide at 10 m intervals across seagrass and unvegetated reef flat at the subtidal boundary at mean low tide (Fig. 1). Four cameras were deployed in the seagrass and another 4 were deployed in each of the unvegetated habitats on either side of the seagrass. More cameras (8) were deployed across the unvegetated habitat than in the seagrass (4) to account for differences in the total area of the 2 habitats. At all locations, unvegetated habitat made up more than twice as much intertidal area than seagrass, thus more replicate cameras were required to characterize the fish occurring there. Cameras secured to 5 lb (~2.3 kg) dive weights were deployed at the seaward edge of the exposed reef flat and recordings continued from the time they were first submerged (~6 cm depth) for ~4 h, until it was approximately slack high tide (~1.6 m depth). A peg with flagging tape was inserted in the field of view 1 m in front of each camera. To avoid using footage with very poor visibility, fish were only counted from footage where the marker was continuously visible throughout the deployment. Water depth was measured using a depth logger (Hobo 13 ft. U20-001-04-Ti) deployed at one location throughout the sampling period.

## Data analysis

Video footage was used to identify fish and measure the relative abundance of each species. Relative abundance was calculated as the maximum number (MaxN) observed in the field of view at the same time (Willis & Babcock 2000, Cappo et al. 2004). This method minimized the likelihood of recounting the same individual multiple times. Each 4 h deployment was divided into 16 stages of 15 min, and fish abundance was averaged across replicate cameras in seagrass and unvegetated habitats to create a mean MaxN (mMaxN) for each species per stage. Intervals

of 15 min were chosen because they allowed for relatively detailed observations of fish movement across tide stages, while reducing the number of zero counts (intervals where no fish were observed) that would have been recorded if fish were evaluated at shorter time scales. Fish, both in schools and as individuals, were usually observed making direct movements past cameras towards the shore, so each 15 min interval represents an independent measurement of relative fish abundance.

Patterns in 'total fish abundance' (the mMaxN of the sum of all species observed) were investigated using a single linear mixed model. Explanatory variables were habitat (seagrass or unvegetated reef flat), tidal depth and location (West Peel, Northwest Peel and Coochiemudlo). A quadratic term for depth (depth<sup>2</sup>) was also included to investigate curvilinear relationships that might result from variability in current speed across the incoming tide. Due to differences in water quality, sedimentation and fishing pressure between western and central bay locations, location was included as a fixed factor, while sampling day (3 location<sup>-1</sup>) was included as a random factor nested in location since sampling was done at comparable times of day, tidal state and weather.

The occurrence of individual species in video footage was very patchy, resulting in frequent zero counts and unevenly distributed data. To account for these issues, species-specific patterns were analysed using a 2-step 'hurdle' model (Fletcher et al. 2005, Zuur et al. 2009). In step 1, mMaxN data were converted to presence/absence during each 15 min observation period and analysed using general linear models with binomial error structures and the logit-link function. Analyses were performed using the lme4 package in R (R Core Team 2017). Step 2 of the hurdle model evaluated the mMaxN of fish per 15 min period, but only for intervals when fish were present. The same explanatory and random variables were used in this step, but data were analysed using linear mixed models with Gaussian error structure and the identity link function. Response variables were ln-transformed when necessary to improve the normality of residuals. The binomial and Gaussian models were fitted using all factors, then least significant terms were removed to achieve the minimal adequate model, as recommended by Crawley (2007) and described by Harborne et al. (2017).

To test the hypothesis that mangrove-associated species are more common in intertidal seagrass habitats than in the unvegetated reef flat, we used the hurdle model analysis described above for 3 abundant and mobile species which are common in the

mangrove forests of Moreton Bay (yellowfin bream *Acanthopagrus australis*, sea mullet *Mugil cephalus* and garfish *Hyporhamphus regularis ardelio*; Morton 1990, Laegdsgaard & Johnson 1995). To test the hypothesis that prey fish would arrive earlier in the tidal cycle than predators, we investigated the most abundant species in each guild with tidal depth as a proxy for arrival time. Common prey species were defined as having a maximum length <20 cm and included common silver-biddy *Gerres subfasciatus*, common hardyhead *Atherinomorus vaigiensis* and striped grunter *Pelates sexlineatus*. Predators were species that primarily consume small fish, including dusky flathead *Platycephalus fuscus*, longtom *Tylosurus gavioloides* and striped barracuda *Sphyræna obtusata* (Baker & Sheaves 2005). Visits (presence/absence and relative abundance) of fishes were assessed by feeding guilds (e.g. prey fish vs. predators) and by individual species. The presence/absence of feeding guilds and species was modelled using step 1 of the hurdle model. The relative abundance of individual species, when present, was only modelled (hurdle model, step 2) if they occurred in  $\geq 9\%$  of all 15 min stages. This limit ensured that trends were only assessed for species with sufficient data.

## RESULTS

### Fish communities on intertidal reef flats

A total of 54 species were observed in the 432 h of video footage recorded in seagrass and unvegetated habitats on reef flats during the incoming tide across all locations (see Table S1 in the Supplement at [www.int-res.com/articles/suppl/m581p135\\_supp.pdf](http://www.int-res.com/articles/suppl/m581p135_supp.pdf)). Of those species, 31 were observed over seagrass and 49 were observed over unvegetated habitat. Videos captured footage of fish that were predominantly benthic carnivores (e.g. Diodontidae, Tetraodontidae, Dasyatidae), omnivores (e.g. Sparidae, Mugilidae) and piscivores (e.g. Platycephalidae, Carangidae, Belonidae). Footage also included piscivores such as spot-tail sharks *Carcharhinus sorrah*, bull sharks *C. leucas*, grey carpetsharks *Chiloscyllium punctatum*, tailor *Pomatomus saltatrix* and golden trevally *Gnathodon speciosus*, but these species were observed in low relative abundances (<10 occurrences of each species). The most common species were silver-biddy *Gerres subfasciatus* (mean MaxN 0.9 per 15 min observation period, seen in 29% of all time stages) yellowfin bream *Acanthopagrus australis* (0.5, 22%), striped grunter *Pelates sexlineatus*

(0.6, 17%), sea mullet *Mugil cephalus* (0.4, 9%) and garfish *Hyporhamphus regularis ardelio* (0.3, 9%).

### Total fish abundance – overall patterns

The strongest predictor of total fish abundance was tidal depth, with most fish arriving early in the tidal cycle (<0.5 m depth; Table 1B, Fig. 3). The number of fish observed was also significantly higher over the unvegetated reef flats than in intertidal seagrass, with ~30% more fish observed over unvegetated habitat on average (Fig. 3).

### Visits by fish associated with mangroves

The presence/absence (hurdle model step 1) of 3 species of mangrove-associated fish on intertidal reef flats was significantly correlated with 1 or more of the explanatory variables, but effects differed among species (Table 1A). Yellowfin bream were observed more frequently early in the tidal cycle at shallow water depths; by contrast, sea mullet and garfish were observed more frequently as depth increased. Sea mullet were also present twice as often over unvegetated habitat, whereas garfish were present only 6% more often over seagrass habitat. Sea mullet and garfish were also present more often at Western Peel Island than at other locations. Patterns in the relative abundance of species associated with mangroves, when present (part 2 of hurdle model), showed that garfish and yellowfin bream were 3 to 5 times more abundant and twice as abundant (consecutively) at Peel Island locations compared to Coochiemudlo Island, and that garfish increased in relative abundance with increasing water depth (Table 1B).

### Visits by predator and prey species

The presence/absence of prey fish and predators on the reef flat (hurdle model step 1) was significantly correlated with 1 or more of the predictor variables, including habitat type for 4 of the 6 species (Table 2). Common silver-biddy and common hardyhead were twice as likely to be present over unvegetated habitat than over seagrass habitat. Common hardyhead also declined in abundance with increasing depth (Table 2, Fig. 4A–C). Conversely, striped grunter were observed more frequently as depth increased (Table 2, Fig. 4G,H). Striped grunter were present more often at Coochiemudlo than at Peel

Table 1. Model coefficient values for (A) the minimal adequate generalized linear mixed-effects model (fixed effects only) for the presence/absence per 15 min observation period of 3 species associated with mangroves and (B) for the minimal adequate linear mixed-effects model (fixed effects only) for the number per 15 min (when present) of the same 3 species and total fish abundance. Coefficients for categorical variables are for seagrass in comparison with unvegetated reef flat (Habitat) and Northwest Peel (N) and Western Peel (W) in comparison with Coochiemudlo (C) (Location). mMaxN: mean maximum number; -: not significant, variable not contained in minimal adequate model; NS: not significant; \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ; NSa: removal of non-significant terms led to a significant increase in model deviance and Akaike information criterion

	Intercept	Habitat (Seagrass)	Depth	Depth <sup>2</sup>	LOCATION (N vs C)	LOCATION (W vs C)	LOCATION (W vs N)
<b>(A) Presence/absence</b>							
Yellowfin bream <i>Acanthopagrus australis</i>	1.978 NS	0.162 NSa	-4.307***	-0.038 NS	-0.288 NSa	-0.116 NSa	0.171 NSa
Sea mullet <i>Mugil cephalus</i>	-2.486 NS	-0.554*	2.625NS	-7.481***	1.797***	2.742***	0.945***
Garfish <i>Hyporhamphus regularis ardelio</i>	-2.209 NS	0.695***	-0.245NS	-1.293*	0.687*	1.485***	0.798***
<b>(B) mMaxN</b>							
Total fish abundance	2.660***	-0.205*	-2.384***	0.743***	-0.160 NSa	-0.074 NSa	0.086 NSa
Yellowfin bream <i>Acanthopagrus australis</i>	0.233*	-	-0.029 NSa	-0.025 NSa	0.488***	0.515***	0.027 NS
Sea mullet <i>Mugil cephalus</i>	-	-	-	-	-	-	-
Garfish <i>Hyporhamphus regularis ardelio</i>	-0.645 NS	-	6.021**	-3.344**	1.819**	2.218***	0.399 NS

Island, whereas common silver-biddy and common hardyhead were more likely to be observed at Western Peel Island (Table 2).

For fish categorized as predators, striped barracuda were present twice as often over seagrass habitat (Table 2, Fig. 4D–F), whereas dusky flathead were more than 3 times more likely to be present over unvegetated habitat (graphics only depict patterns in presence/absence or relative abundance across depth since other results were binary). Striped

barracuda were also observed more frequently with increasing depth. There was a higher probability of observing longtom and flathead at Peel Island locations, while striped barracuda were present more often at Coochiemudlo Island (Table 2).

All predators, when present (hurdle model, part 2), increased in relative abundance with increasing depth, regardless of habitat (Table 3, Fig. 5A). By contrast, all prey fish decreased in relative abundance with increasing water depth, regardless of habitat type (Table 3, Fig. 5B). Of the individual species modelled, only striped grunter and common silver-biddy were common enough to evaluate trends in relative abundance. Striped grunter were more abundant over seagrass habitat, and were most abundant at the mid-point of the incoming tide (Table 3, Fig. 5D,E). By contrast, common silver-biddy were least abundant at the mid-point of the incoming tide (Table 3, Fig. 5C). Striped grunter were more abundant at Northwest Peel and Coochiemudlo islands, whereas common silver-biddy were more abundant at Northwest Peel Island.

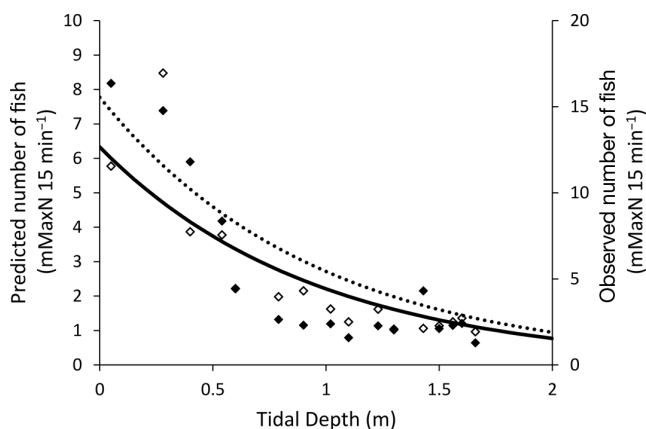


Fig. 3. Relationship between the depth of the tide and the predicted number of fish visiting the reef flat for total fish abundance. Predicted values from statistical models are on the left-hand axis (the black line represents seagrass and the dotted line unvegetated reef flat). Observations are on the right hand axis (black diamonds are seagrass and open diamonds unvegetated reef flat). mMaxN: mean maximum number

## DISCUSSION

### Movement of fish across intertidal coral reef seascapes

Inshore coral reef seascapes function as habitat networks rather than as a series of isolated patches

Table 2. Model coefficient values for minimal adequate generalized linear mixed-effects model (fixed effects only) for the presence/absence per 15 min observation period of the 3 most abundant prey and predator species, and all prey and predator species combined, on the coral reef flat during the incoming tide. Coefficients for categorical variables are for seagrass in comparison with unvegetated reef flat (Habitat) and Northwest Peel (N) and Western Peel (W) in comparison with Coochiemudlo (C) (Location). -: not significant, variable not contained in minimal adequate model; NS: not significant; \*p < 0.05; \*\*p < 0.01; \*\*\*p < 0.001; NSa: removal of non-significant terms led to a significant increase in model deviance and Akaike information criterion

	Intercept	Habitat (Seagrass)	Depth	Depth <sup>2</sup>	LOCATION (N vs C)	LOCATION (W vs C)	LOCATION (W vs N)
Prey fish	4.675***	-2.298***	0.507 NS	-0.272 NS	-2.311***	-2.737***	-0.42 NS
Predators	0.960*	0.011 NS	-0.634 NS	-0.243 NS	-0.555 NS	0.101 NS	0.657*
<b>Predators</b>							
Longtom	-0.294 NS	-	-2.175 NSa	-0.114 NSa	1.21*	1.464**	0.254 NS
<i>Tylosurus gavioloides</i>							
Striped barracuda	-6.046***	4.341**	6.265*	-	-1.818***	-1.696***	0.121 NS
<i>Sphyaena obtusata</i>							
Flathead	-0.249 NS	-1.826***	-2.446 NSa	-0.839 NSa	0.984 NS	1.426*	0.442 NS
<i>Platycephalus fuscus</i>							
<b>Prey fish</b>							
Silver-biddy	1.775**	-2.729***	-	-	0.849*	-0.557 NS	-1.405***
<i>Gerres subfasciatus</i>							
Hardyhead	-1.413 NS	-1.005*	-4.342*	-	1.287 NS	3.198***	1.911***
<i>Atherinomorus vaigiensis</i>							
Striped grunter	1.616*	-	3.169*	-1.726*	-3.635***	-4.505***	-0.871*
<i>Pelates sexlineatus</i>							

(Sheaves 2009, Gillis et al. 2014, Engelhard et al. 2017). Recent reviews suggest that our understanding of habitat function in these areas will greatly improve if we can identify the efficacy and location of migration pathways for nekton (Berkström et al. 2012, Green et al. 2015, Nagelkerken et al. 2015, Olds et al. 2016). This study is the first to evaluate whether fish use specific benthic habitats as corridors when moving into intertidal areas, and contributes to the debate on the efficacy of shallow-water habitats as predator refuges. Our data suggest that continuous seagrass habitats may sometimes function as corridors for fish, but that their use varies among species. Furthermore, while previous literature on fish arrival times in intertidal habitats suggests that small fishes move into shallow waters to escape predation (Bretsch & Allen 2006, Ellis & Bell 2008), our results are consistent with recent studies that question this paradigm (Baker & Sheaves 2006, Tobin et al. 2014). Various species of prey fish were present across the tidal flux, and the presence of predators was not always associated with increasing depth.

### Continuous seagrass beds as corridors

The hypothesis that continuous seagrass habitat functions as a corridor for fish movement was supported for only a few of the focal species. More fish were observed moving over unvegetated habitat,

and abundant, highly mobile species that are commonly associated with local mangroves, such as yellowfin bream and sea mullet, did not occur more often over seagrass. More species may prefer to move across the unvegetated reef flat to forage since the hard substrate supports many benthic invertebrates, and some fish such as sea mullet and trevally were observed foraging there (Davis et al. 2015). However, visits by garfish, striped barracuda and striped grunter, which are also found in mangroves in Morton Bay (Morton 1990, Laegdsgaard & Johnson 1995), were positively associated with seagrass habitat. Seagrass offers important resources for migrating fish, including preferred food sources for herbivores (Verweij et al. 2006) and benthic carnivores (Robblee & Zieman 1984, Nagelkerken et al. 2000), as well as increased habitat complexity (Jordan et al. 1997). For example, garfish and striped grunter consume seagrass (Connolly 2003, Carseldine & Tibbetts 2005) and invertebrate prey associated with seagrass habitat (Sanchez-Jerez et al. 2002). Striped barracuda typically feed on small pelagic fish and prawns (Blaber et al. 1990), and increased habitat complexity in seagrass beds can be advantageous for both the foraging and sheltering of small barracuda (De Sylva 1963).

Visits by fish may be inconsistent between habitat types for several reasons. Although benthic invertebrates use habitat corridors (Darcy & Eggleston 2005), fish may be less dependent on them because their

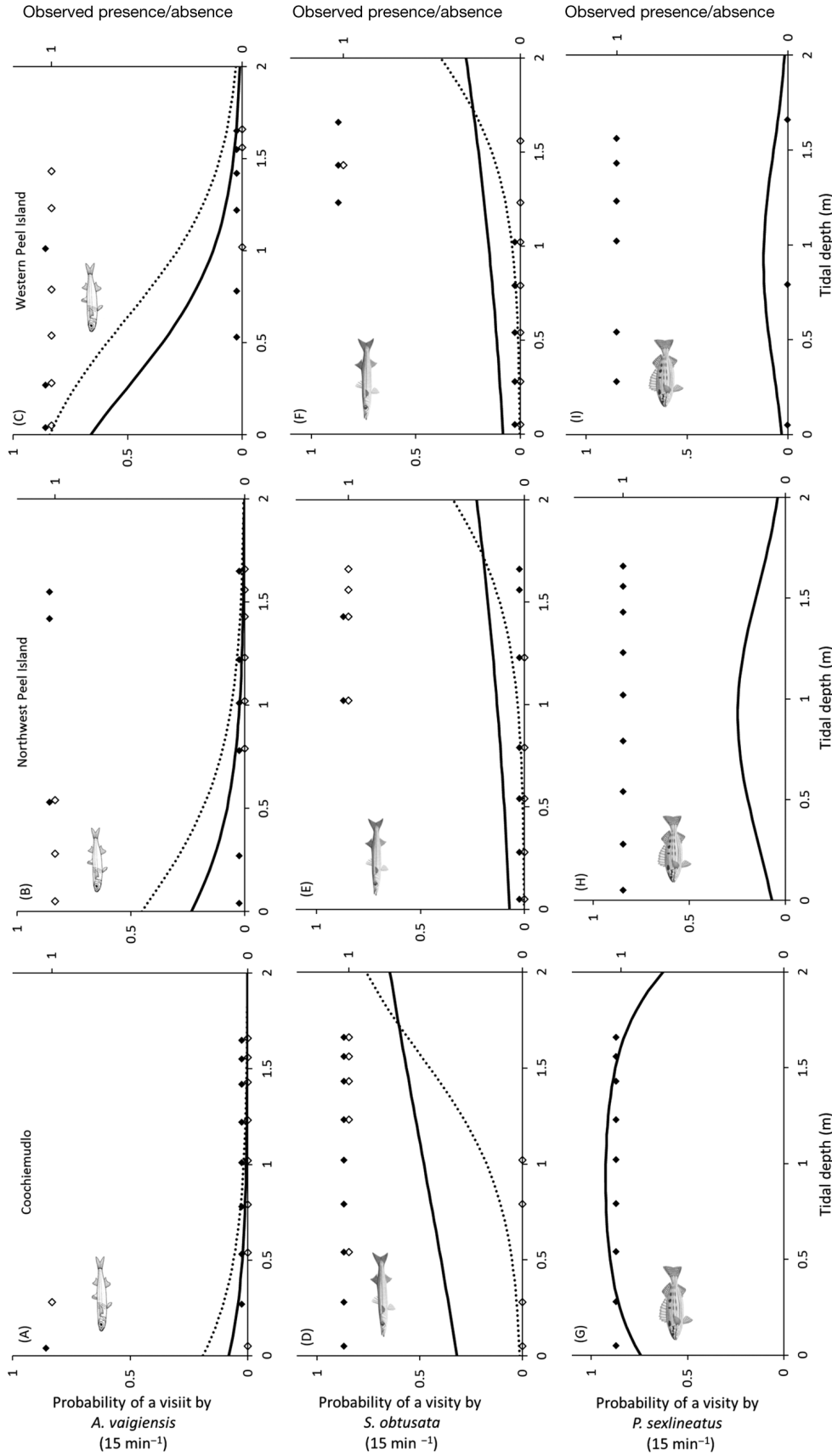


Fig. 4. Relationship between the depth of the tide and the presence/absence of (A–C) hardyhead *Atherinomorus vaigiensis*, (D–F) striped barracuda *Sphyraena obtusata* and (G–I) striped grunter *Pelates sexlineatus* as predicted by the model (left-hand axis) and observed on video (right-hand axis) at each location. Predicted values from statistical models are illustrated by a black line for seagrass and a dotted line for unvegetated reef flat (A–F). In G–I the black line represents all habitats since there was no interaction with habitat type for striped grunter. Observations are illustrated by black diamonds for seagrass habitat and open diamonds for unvegetated reef flat (A–F). In G–I black diamonds represent all habitats. For observations, a score of 1 indicates that fish were recorded as present in 1 or more of the video replicates and 0 indicates the species was never recorded



Table 3. Model coefficient values for minimal adequate linear mixed-effects model (fixed effects only) for the number of fish per 15 min observation period (when present) of 2 prey species, and for prey and predators combined. Coefficients for categorical variables are for seagrass in comparison with unvegetated reef flat (Habitat) and Northwest Peel (N) and Western Peel (W) in comparison with Coochiemudlo (C) (Location). -: not significant, variable not contained in minimal adequate model; NS: not significant; \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$

	Intercept	Habitat (Seagrass)	Depth	Depth <sup>2</sup>	LOCATION (N vs C)	LOCATION (W vs C)	LOCATION (W vs N)
Prey fish	1.256***	–	–0.851*	–	0.177 NS	–0.059 NS	–0.235*
Predators	–0.066 NS	–	0.982*	–0.474*	0.019 NS	0.252*	0.233*
Silver-biddy	–0.301 NS	–	–1.703**	0.852**	0.954***	0.219 NS	–0.722***
<i>Gerres subfasciatus</i>							
Striped grunter	–1.159***	0.429*	1.892*	–1.056**	–0.163 NS	–0.619*	–0.455***
<i>Pelates sexlineatus</i>							

movements are better facilitated by hydrodynamics and less restricted by benthic structure. Alternatively, temporal variability in the relative abundance of fish may have obscured results for corridor use. Not all fishes make successive tidal or even diel migrations. For example, sea mullet only access mangrove creeks on 4 wk cycles (Meynecke et al. 2008), and schooling species, which were common in our study, introduce high variability to fish counts in intertidal areas (Connolly 1994). Moreover, some fishes make large-scale movements among reefs (Pittman et al. 2014), perhaps resulting in variable numbers of fish moving into intertidal areas at different times. For example, adult yellowfin bream in Moreton Bay can make movements of 10–90 km to form spawning aggregations at surf bars, although they otherwise occupy relatively narrow home ranges (0–6 km; Pollock 1982).

The use of corridors may vary among locations due to differences in the physical characteristics of the corridor habitat. Seagrass characteristics such as shoot density, biomass and canopy height affect the community structure of fish (Pogoreutz et al. 2012, Ray et al. 2014), either because of changes in the relative risk of predation (Smith et al. 2011) or availability of food sources (Attrill et al. 2000). This may explain why visits by sea mullet, yellowfin bream and garfish were more common at Peel Island compared to Coochiemudlo Island. The physical characteristics of seagrass or unvegetated reef flat habitat at Coochiemudlo Island might have been less favourable for mobile species that make tidal movements to mangroves because this area is closer to the mainland, has lower coral cover and higher turbidity (Olds et al. 2012b). Additionally, because Coochiemudlo Island is located directly adjacent to the mainland, high fishing pressure may explain the lower number of recreationally targeted species such as bream compared to Peel Island, which is partially protected by a no-take marine reserve.

Our results suggest that fish can use seagrass habitat as a corridor when migrating between subtidal habitats and intertidal mangroves, but that the importance of seagrass corridors depends on the species and location sampled. Future studies should therefore investigate corridor use by fish across longer time scales (i.e. across many days, diel cycles and seasons) and on reef flats with different physical characteristics, to better elucidate patterns in habitat use. Moreover, although our study evaluates the arrival of fishes (that occurred in local mangroves in prior studies) to potential corridor habitats, it cannot confirm that those individuals also arrived at the mangrove edge. To confirm corridor use, a tagging study on these same species would be required.

#### Predator and prey fish arrival times

Shallow intertidal habitats in coastal zones have often been referred to as refuges from predation for small and juvenile fish (Baltz et al. 1993, Gibson et al. 2002, Rypel et al. 2007, Ryer et al. 2010), although recent studies have suggested otherwise (Sheaves 2001, Baker & Sheaves 2007, 2009, Dorenbosch et al. 2009, Tobin et al. 2014). While this paradigm may hold true in some locations, increasing evidence suggests that shallow waters (<1 m) in tropical and subtropical inshore environments are frequented by predators that could exert significant predation pressure on small fishes (Baker & Sheaves 2009). Our results confirm that, in general, prey fish were more abundant at shallow depths and predators were more abundant later in the tidal cycle; however, predatory fishes, which are often responsible for high rates of piscivory, such as flat-head and longtom (Baker & Sheaves 2005), occurred throughout the tidal cycle at shallow depths (<1.5 m).

Fishes with compressed body types such as flat-head and longtom may arrive in intertidal habitats at

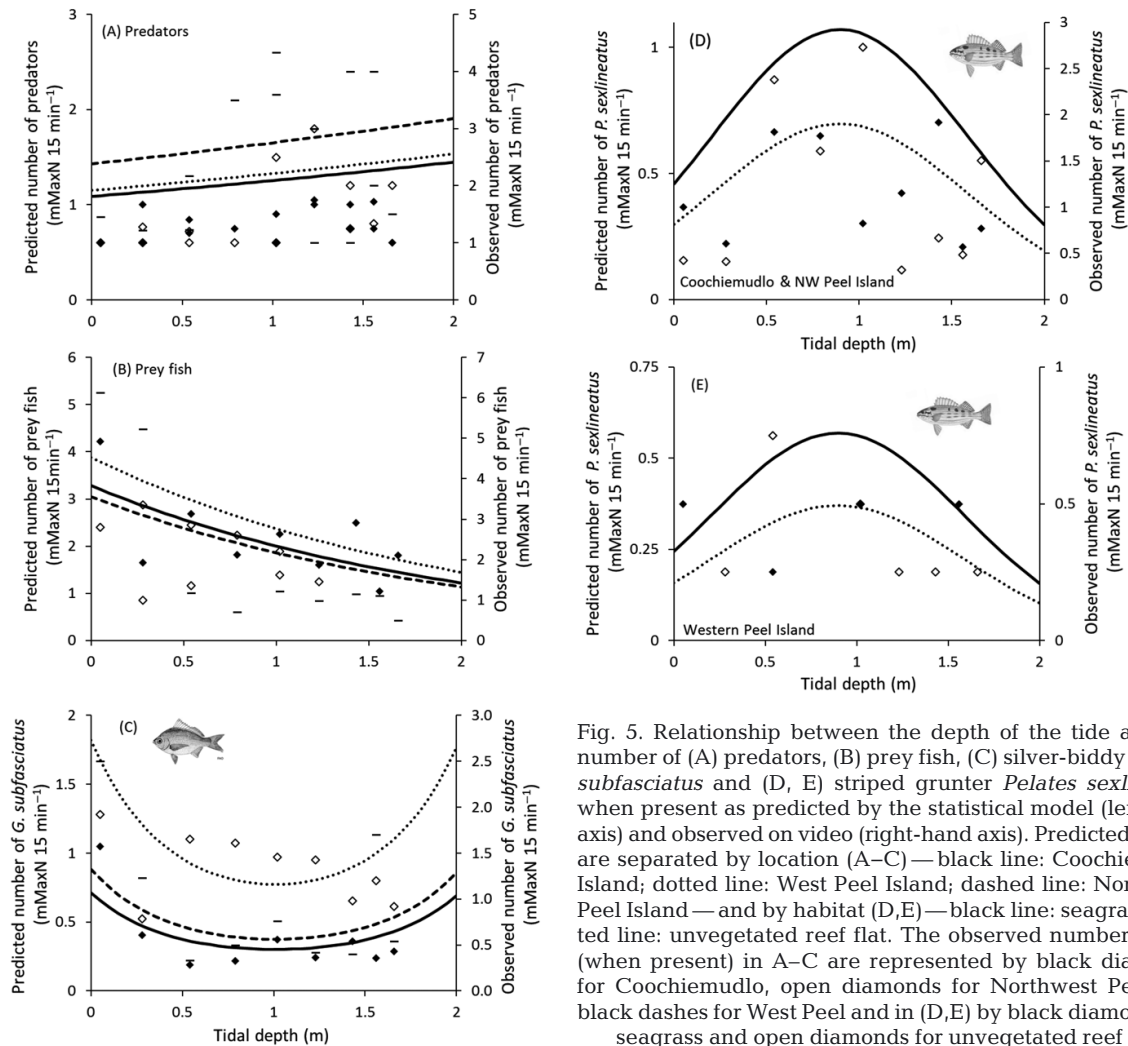


Fig. 5. Relationship between the depth of the tide and the number of (A) predators, (B) prey fish, (C) silver-biddy *Gerres subfasciatus* and (D, E) striped grunter *Pelates sexlineatus* when present as predicted by the statistical model (left-hand axis) and observed on video (right-hand axis). Predicted values are separated by location (A–C) — black line: Coochiemudlo Island; dotted line: West Peel Island; dashed line: Northwest Peel Island — and by habitat (D,E) — black line: seagrass; dotted line: unvegetated reef flat. The observed number of fish (when present) in A–C are represented by black diamonds for Coochiemudlo, open diamonds for Northwest Peel and black dashes for West Peel and in (D,E) by black diamonds for seagrass and open diamonds for unvegetated reef flat

shallow depths to take advantage of increased feeding opportunities. Flathead are ambush predators (Platell & Potter 1998), and arriving early in the flooding tide affords them maximum time to bury in the sand in preparation for feeding. Longtom are pelagic predators (Boughton et al. 1991), and while not dorso-ventrally compressed like flathead, have a narrow anguilliform body shape which also facilitates feeding in shallow water. Baker & Sheaves (2006) observed high abundances of flathead in shallow waters (0.01–0.6 m) of tropical estuaries, and fresh prey fish were present in the gut contents of both flathead and longtom collected from these areas (Baker & Sheaves 2005). Conversely, striped barracuda, which were more abundant later in the tidal cycle, are smaller, travel in schools (May & Maxwell 1986) and might avoid potentially antagonistic interactions with other predators such as longtom and flathead by arriving on intertidal reef flats later in the tidal cycle.

Visits by piscivore and prey species varied among locations, but this variability did not alter the effects of water depth. Striped grunter and striped barracuda may be more common at Coochiemudlo Island due to their preference for seagrass habitat. Seagrass in turbid water environments in Moreton Bay, like Coochiemudlo Island, has wider blades that help it remain resilient to low water quality events (Gibbes et al. 2014). Thus, seagrass at this location may provide better habitat for invertebrate foods (Troch et al. 2005) and increased shelter.

Although our results show that small fish and their predators are both present in very shallow waters in intertidal habitats, prey fish were often more abundant at shallow depths. Small fish might have a relatively lower predation risk, or expend less energy avoiding predation, in shallow waters (Baker & Sheaves 2007). Indeed, the negative relationship between the presence of common hardyhead and the

relative abundance of common silver-biddy with increasing tidal depth does suggest that they might focus transitional movements to the intertidal at the shallowest of depths (<0.2 m). Nonetheless, both common silver-biddy and striped grunter occurred throughout the remainder of the tidal cycle, so the presence of small fishes in intertidal habitats was generally not restricted by water depth or the presence of predators. Additionally, the presence of piscivorous fishes in the shallow intertidal may equally be driven by a need to escape predation by even larger predators, and less so for feeding. The paradigm that shallow waters are not frequented by predators was not supported by our results, and should therefore be re-evaluated across a broader range of environments (*sensu* Sheaves 2001).

## CONCLUSION

The results of this and other recent studies (Ellis & Bell 2008, Becker et al. 2011, 2012, Harborne et al. 2016) suggest that the factors affecting the movements of fish in shallow environments vary spatially, across tidal state, among species and between similar ecosystems in different settings. Our results support recent assertions that shallow-water habitats may be more important for predators than previously thought, especially in tropical and subtropical estuarine settings in the Pacific Ocean and Caribbean Sea (Baker & Sheaves 2005, 2006, Dorenbosch et al. 2009, Tobin et al. 2014). We propose that habitat corridors may facilitate the movement of some species of fish among marine habitats, but more research is needed to investigate how movement pathways of fish change in different seascapes over longer periods. Shallow coral reefs are particularly vulnerable to impacts from coastal development and the effects of climate change (Harborne 2013); to improve conservation planning for these ecosystems, it is essential that we develop a better understanding of how biotic and abiotic factors interact to shape patterns of animal migration and habitat use across coastal seascapes.

*Acknowledgements.* We thank A. Budarf, S. Engelhard, B. Gilby, C. Henderson, R. Win and the staff at Moreton Bay Research Station for their assistance. This research was supported by an Australian Research Council (ARC) Linkage grant (to R.M.C. and K.A.P.) in collaboration with the Queensland Government. A.R.H. was funded by the ARC through fellowship DE120102459. This is contribution 71 from the Marine Education and Research Center in the Institute for Water and Environment at Florida International University.

## LITERATURE CITED

- ✦ Attrill MJ, Strong JA, Rowden AA (2000) Are macroinvertebrate communities influenced by seagrass structural complexity? *Ecography* 23:114–121
- ✦ Baker R, Sheaves M (2005) Redefining the piscivore assemblage of shallow estuarine nursery habitats. *Mar Ecol Prog Ser* 291:197–213
- ✦ Baker R, Sheaves M (2006) Visual surveys reveal high densities of large piscivores in shallow estuarine nurseries. *Mar Ecol Prog Ser* 323:75–82
- ✦ Baker R, Sheaves M (2007) Shallow-water refuge paradigm: conflicting evidence from tethering experiments in a tropical estuary. *Mar Ecol Prog Ser* 349:13–22
- ✦ Baker R, Sheaves M (2009) Overlooked small and juvenile piscivores dominate shallow-water estuarine 'refuges' in tropical Australia. *Estuar Coast Shelf Sci* 85:618–626
- ✦ Baltz DM, Rakocinski C, Fleeger JW (1993) Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environ Biol Fishes* 36:109–126
- ✦ Banikas EM, Thompson JS (2012) Predation risk experienced by mummichog, *Fundulus heteroclitus*, in intertidal and subtidal salt marsh habitats. *Estuaries Coasts* 35:1346–1352
- ✦ Becker A, Cowley PD, Whitfield AK, Järnegren J, Næsje TF (2011) Diel fish movements in the littoral zone of a temporarily closed South African estuary. *J Exp Mar Biol Ecol* 406:63–70
- ✦ Becker A, Coppinger C, Whitfield AK (2012) Influence of tides on assemblages and behaviour of fishes associated with shallow seagrass edges and bare sand. *Mar Ecol Prog Ser* 456:187–199
- ✦ Beger M, Linke S, Watts M, Game E, Treml E, Ball I, Possingham HP (2010) Incorporating asymmetric connectivity into spatial decision making for conservation. *Conserv Lett* 3:359–368
- ✦ Berkström C, Gullström M, Lindborg R, Mwandya AW, Yahya SAS, Kautsky N, Nyström M (2012) Exploring 'knowns' and 'unknowns' in tropical seascape connectivity: a review with insights from East African coral reefs. *Estuar Coast Shelf Sci* 107:1–21
- ✦ Blaber S, Milton D, Rawlinson N, Tiroba G, Nichols P (1990) Diets of lagoon fishes of the Solomon Islands: predators of tuna baitfish and trophic effects of baitfishing on the subsistence fishery. *Fish Res* 8:263–286
- ✦ Boström C, Pittman SJ, Simenstad C, Kneib RT (2011) Seascape ecology of coastal biogenic habitats: advances, gaps, and challenges. *Mar Ecol Prog Ser* 427:191–217
- ✦ Boughton DA, Collette BB, McCune AR (1991) Heterochrony in jaw morphology of needlefishes (Teleostei: Belontiidae). *Syst Biol* 40:329–354
- ✦ Bretsch K, Allen DM (2006) Tidal migrations of nekton in salt marsh intertidal creeks. *Estuaries Coasts* 29:474–486
- ✦ Cappo M, Speare P, De'ath G (2004) Comparison of baited remote underwater video stations (BRUVS) and prawn (shrimp) trawls for assessments of fish biodiversity in inter-reefal areas of the Great Barrier Reef Marine Park. *J Exp Mar Biol Ecol* 302:123–152
- ✦ Carseldine L, Tibbetts I (2005) Dietary analysis of the herbivorous hemiramphid *Hyporhamphus regularis ardelio*: an isotopic approach. *J Fish Biol* 66:1589–1600
- ✦ Caselle JE, Warner RR (1996) Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. *Ecology* 77:2488–2504

- Chubb CF, Potter IC, Grant CJ, Lenanton RCJ, Wallace J (1981) Age structure, growth rates and movements of sea mullet, *Mugil cephalus* L., and yellow-eye mullet, *Aldrichetta forsteri* (Valenciennes), in the Swan-Avon river system, Western Australia. *Aust J Mar Freshw Res* 32:605–628
- Connolly R (1994) A comparison of fish assemblages from seagrass and unvegetated areas of a southern Australian estuary. *Aust J Mar Freshw Res* 45:1033–1044
- Connolly RM (2003) Differences in trophodynamics of commercially important fish between artificial waterways and natural coastal wetlands. *Estuar Coast Shelf Sci* 58: 929–936
- Crawley MJ (2007) *The R Book*, 2nd edn. John Wiley & Sons Ltd., Chichester
- Darcy MC, Eggleston DB (2005) Do habitat corridors influence animal dispersal and colonization in estuarine systems? *Landsc Ecol* 20:841–855
- Davis J, Pitt K, Fry B, Olds A, Connolly R (2014) Seascape-scale trophic links for fish on inshore coral reefs. *Coral Reefs* 33:897–907
- Davis J, Pitt K, Connolly R, Fry B (2015) Community structure and dietary pathways for invertebrates on intertidal coral reef flats. *Food Webs* 3:7–16
- De Troch M, Vandepitte L, Raes M, Suàrez-Morales E, Vincx M (2005) A field colonization experiment with meiofauna and seagrass mimics: effect of time, distance and leaf surface area. *Mar Biol* 148:73–86
- Dennison WC, Abal EG (1999) Moreton Bay study: a scientific basis for the healthy waterways campaign. South East Queensland Regional Water Quality Management Strategy Team, Brisbane
- De Sylva DP (1963) Systematics and life history of the great barracuda, *Sphyræna barracuda* (Walbaum). *Stud Trop Oceanogr* 1:1–79
- Dorenbosch M, Grol MGG, de Groene A, van der Velde G, Nagelkerken I (2009) Piscivore assemblages and predation pressure affect relative safety of some back-reef habitats for juvenile fish in a Caribbean bay. *Mar Ecol Prog Ser* 379:181–196
- Ellis WL, Bell SS (2008) Tidal influence on a fringing mangrove intertidal fish community as observed by *in situ* video recording: implications for studies of tidally migrating nekton. *Mar Ecol Prog Ser* 370:207–219
- Engelhard SL, Huijbers CM, Stewart-Koster B, Olds AD, Schlacher TA, Connolly RM (2017) Prioritising seascape connectivity in conservation using network analysis. *J Appl Ecol* 54:1130–1141
- Fletcher D, MacKenzie D, Villouta E (2005) Modelling skewed data with many zeros: a simple approach combining ordinary and logistic regression. *Environ Ecol Stat* 12:45–54
- Gibbes B, Grinham A, Neil D, Olds A and others (2014) Moreton Bay and its estuaries: a sub-tropical system under pressure from rapid population growth. In: Wolanski E (ed) *Estuaries of Australia in 2050 and beyond*. Estuaries of the world. Springer, Dordrecht, p 203–222
- Gibson RN, Robb L, Wennhage H, Burrows MT (2002) Ontogenetic changes in depth distribution of juvenile flatfishes in relation to predation risk and temperature on a shallow-water nursery ground. *Mar Ecol Prog Ser* 229: 233–244
- Gilbert-Norton L, Wilson R, Stevens JR, Beard KH (2010) A meta-analytic review of corridor effectiveness. *Conserv Biol* 24:660–668
- Gillis LG, Bouma TJ, Jones CG, van Katwijk MM and others (2014) Potential for landscape-scale positive interactions among tropical marine ecosystems. *Mar Ecol Prog Ser* 503:289–303
- Green AL, Maypa AP, Almany GR, Rhodes KL and others (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biol Rev Camb Philos Soc* 90:1215–1247
- Hammerschlag N, Heithaus MR, Serafy JE (2010) Influence of predation risk and food supply on nocturnal fish foraging distributions along a mangrove–seagrass ecotone. *Mar Ecol Prog Ser* 414:223–235
- Harborne AR (2013) The ecology, behaviour and physiology of fishes on coral reef flats, and the potential impacts of climate change. *J Fish Biol* 83:417–447
- Harborne AR, Talwar B, Brooks EJ (2016) The conservation implications of spatial and temporal variability in the diurnal use of Bahamian tidal mangrove creeks by transient predatory fishes. *Aquat Conserv* 26:202–211
- Harborne AR, Selwyn J, Lawson J, Gallo M (2017) Environmental drivers of diurnal visits by transient predatory fishes to Caribbean patch reefs. *J Fish Biol* 90:265–282
- Irlandi E, Crawford M (1997) Habitat linkages: the effect of intertidal saltmarshes and adjacent subtidal habitats on abundance, movement, and growth of an estuarine fish. *Oecologia* 110:222–230
- Jones DL, Walter JF, Brooks EN, Serafy JE (2010) Connectivity through ontogeny: fish population linkages among mangrove and coral reef habitats. *Mar Ecol Prog Ser* 401: 245–258
- Jordan F, Bartolini M, Nelson C, Patterson PE, Soulen HL (1997) Risk of predation affects habitat selection by the pinfish *Lagodon rhomboides* (Linnaeus). *J Exp Mar Biol Ecol* 208:45–56
- Kimball M, Able K (2012) Tidal migrations of intertidal salt marsh creek nekton examined with underwater video. *Northeast Nat* 19:475–486
- Krumme U (2009) Diel and tidal movements by fish and decapods linking tropical coastal ecosystems. In: Nagelkerken I (ed) *Ecological connectivity among tropical coastal ecosystems*. Springer, New York, NY, p 271–324
- Laegdsgaard P, Johnson CR (1995) Mangrove habitats as nurseries: unique assemblages of juvenile fish in subtropical mangroves in eastern Australia. *Mar Ecol Prog Ser* 126:67–81
- Lugendo BR, Nagelkerken I, Jiddawi N, Mgaya YD, Van Der Velde G (2007) Fish community composition of a tropical nonestuarine embayment in Zanzibar, Tanzania. *Fish Sci* 73:1213–1223
- Lyons M, Phinn S, Roelfsema C (2011) Integrating Quickbird multi-spectral satellite and field data: mapping bathymetry, seagrass cover, seagrass species and change in Moreton Bay, Australia in 2004 and 2007. *Remote Sensing* 3(1):42–64
- May JL, Maxwell JGH (1986) Trawl fish from temperate waters of Australia. CSIRO Division of Fisheries Research, Hobart
- Melville AJ, Connolly RM (2003) Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. *Oecologia* 136:499–507
- Meynecke JO, Poole GC, Werry J, Lee SY (2008) Use of PIT tag and underwater video recording in assessing estuarine fish movement in a high intertidal mangrove and salt marsh creek. *Estuar Coast Shelf Sci* 79:168–178

- Micheli F, Peterson CH (1999) Estuarine vegetated habitats as corridors for predator movements. *Conserv Biol* 13: 869–881
- Morton R (1990) Community structure, density and standing crop of fishes in a subtropical Australian mangrove area. *Mar Biol* 105:385–394
- Nagelkerken I, Dorenbosch M, Verberk WCEP, Cocheret de la Morinière E, van der Velde G (2000) Day-night shifts of fishes between shallow-water biotopes of a Caribbean bay, with emphasis on the nocturnal feeding of Haemulidae and Lutjanidae. *Mar Ecol Prog Ser* 194:55–64
- Nagelkerken I, Bothwell J, Nemeth RS, Pitt JM, van der Velde G (2008) Interlinkage between Caribbean coral reefs and seagrass beds through feeding migrations by grunts (Haemulidae) depends on habitat accessibility. *Mar Ecol Prog Ser* 368:155–164
- Nagelkerken I, Sheaves M, Baker R, Connolly R (2015) The seascape nursery: a novel spatial approach to identify and manage nurseries for coastal marine fauna. *Fish Fish* 16:362–371
- Nanjo K, Nakamura Y, Horinouchi M, Kohno H, Sano M (2011) Predation risks for juvenile fishes in a mangrove estuary: a comparison of vegetated and unvegetated microhabitats by tethering experiments. *J Exp Mar Biol Ecol* 405:53–58
- Olds A, Connolly R, Pitt K, Maxwell P (2012a) Habitat connectivity improves reserve performance. *Conserv Lett* 5: 56–63
- Olds AD, Connolly RM, Pitt KA, Maxwell PS (2012b) Primacy of seascape connectivity effects in structuring coral reef fish assemblages. *Mar Ecol Prog Ser* 462:191–203
- Olds AD, Connolly RM, Pitt KA, Pittman SJ and others (2016) Quantifying the conservation value of seascape connectivity: a global synthesis. *Glob Ecol Biogeogr* 25:3–15
- Pittman S, Olds A (2014) Seascape ecology of fishes on coral reefs. In: Mora C (ed) *Ecology of fishes on coral reefs*. Cambridge University Press, Cambridge, p 275–282
- Pittman SJ, McAlpine CA, Pittman KM (2004) Linking fish and prawns to their environment: a hierarchical landscape approach. *Mar Ecol Prog Ser* 283:233–254
- Pittman SJ, Monaco ME, Friedlander AM, Legare B and others (2014) Fish with chips: tracking reef fish movements to evaluate size and connectivity of Caribbean marine protected areas. *PLOS ONE* 9:e96028
- Platell ME, Potter IC (1998) Distributions, size compositions and diets of two abundant benthic ambush-feeding teleosts in coastal waters of south-western Australia. *J Mar Biol Assoc UK* 78:587–608
- Pogoreutz C, Kneer D, Litaay M, Asmus H, Ahnelt H (2012) The influence of canopy structure and tidal level on fish assemblages in tropical Southeast Asian seagrass meadows. *Estuar Coast Shelf Sci* 107:58–68
- Pollock BR (1982) Movements and migrations of yellowfin bream, *Acanthopagrus australis* (Günther), in Moreton Bay, Queensland as determined by tag recoveries. *J Fish Biol* 20:245–252
- Ray BR, Johnson MW, Cammarata K, Smee DL (2014) Changes in seagrass species composition in north-western Gulf of Mexico estuaries: effects on associated seagrass fauna. *PLOS ONE* 9:e107751
- Robblee MB, Zieman JC (1984) Diel variation in the fish fauna of a tropical seagrass feeding ground. *Bull Mar Sci* 34:335–345
- Ryer CH, Laurel BJ, Stoner AW (2010) Testing the shallow water refuge hypothesis in flatfish nurseries. *Mar Ecol Prog Ser* 415:275–282
- Rypel AL, Layman CA, Arrington DA (2007) Water depth modifies relative predation risk for a motile fish taxon in Bahamian tidal creeks. *Estuaries Coasts* 30:518–525
- Sanchez Jerez P, Gillanders B, Kingsford M (2002) Spatial variation in abundance of prey and diet of trumpeter (*Pelates sexlineatus*: Teraponidae) associated with *Zostera capricorni* seagrass meadows. *Austral Ecol* 27:200–210
- Sheaves M (2001) Are there really few piscivorous fishes in shallow estuarine habitats? *Mar Ecol Prog Ser* 222: 279–290
- Sheaves M (2009) Consequences of ecological connectivity: the coastal ecosystem mosaic. *Mar Ecol Prog Ser* 391: 107–115
- Smith MJ, Betts MG, Forbes GJ, Kehler DG, Bourgeois MC, Flemming SP (2011) Independent effects of connectivity predict homing success by northern flying squirrel in a forest mosaic. *Landscape Ecol* 26:709–721
- R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Tobin AJ, Mapleston A, Harry AV, Espinoza M (2014) Big fish in shallow water; use of an intertidal surf-zone habitat by large-bodied teleosts and elasmobranchs in tropical northern Australia. *Environ Biol Fishes* 97:821–838
- Unsworth RKF, De León PS, Garrard SL, Jompa J, Smith DJ, Bell JJ (2008) High connectivity of Indo-Pacific seagrass fish assemblages with mangrove and coral reef habitats. *Mar Ecol Prog Ser* 353:213–224
- Verweij MC, Nagelkerken I, de Graaff D, Peeters M, Bakker EJ, van der Velde G (2006) Structure, food and shade attract juvenile coral reef fish to mangrove and seagrass habitats: a field experiment. *Mar Ecol Prog Ser* 306: 257–268
- Werner EE, Hall DJ (1988) Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* 69:1352–1366
- Willis TJ, Babcock RC (2000) A baited underwater video system for the determination of relative density of carnivorous reef fish. *Mar Freshw Res* 51:755–763
- Zuur A, Ieno E, Walker N, Saveliev A, Smith G (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York, NY